Light sharing among different forest strata for sustainable management of vegetation and regeneration

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Summary

There is a current trend towards managing forests with multiple objectives, in particular to preserve or increase biodiversity and sustainability. There is renewed interest in understorey vegetation as a way both to increase the number of species and, indirectly, to favour fauna, including game, or improve soil quality. However, this stratum of herbaceous or shrubby species can also compete with young tree seedling and jeopardise tree regeneration. Hence a compromise has to be found among the different management objectives for the forest and in particular the understorey.

Light is one of the main environmental factors controlling ecological and biological processes in forests. For example, light quantity and light quality control the success of seed germination and the establishment and growth of tree seedlings in the understorey. Light also promotes the development of the floor vegetation, the composition of which varies with site conditions in addition to light. Modifying light availability in the understorey, for example with thinning operations, thus interferes with tree regeneration and flora cover and composition. The understorey plants can intercept a significant fraction of the light and so the resulting amount of light available for tree seedlings varies greatly depending on species and composition of the floor vegetation. Light is successively intercepted and transmitted by the different strata composing the forest stand, i.e. overstorey trees, midstorey trees, shrubs and herbaceous species. The different strata interact, the development of each one being controlled by the others, often through modification of light availability. Foresters have to control this chain of light sharing to steer forest stands towards different objectives. We report results concerning the light sharing chain and discuss their implications for management.

Introduction

For a long time forests of the temperate zone have been managed solely for the production of wood. In his book on sylviculture, Perrin (1963) noted that "earlier foresters considered herbs as enemies and managed stands for a clean soil", a clean soil meaning without any vegetation, "evidence that the trees were using all the available radiation". The current trend is more towards managing forests with multiple objectives, in particular to preserve or increase biodiversity and sustainability. The understorey vegetation has received renewed attention as a way both to increase the number of species in the forest, and indirectly, to favour fauna, including game, or improve soil quality. However, this stratum of herbaceous or shrubby species can also compete with young tree seedling and so jeopardise tree regeneration. In addition, a dense layer of vegetation, particularly thorny species, is not always appreciated by urban forest walkers. Hence a compromise has to be found among the different managing objectives for the forest and in particular the understorey. Foresters need tools to implement such forest management.

Light is one of the main environmental factors controlling ecological and biological processes in forests. Clearly, factors such as soil water availability, nutrients and temperatures are also fundamental, but these are all linked to some extent to light availability (Barbier et al., 2008). Light and water from rainfall are both related to tree crown density and gap percentage in the canopy, so that an increased light penetration implies an increase in rainfall reaching the forest floor. Less light or water interception by the canopy in turn means a smaller leaf area index (LAI) and so lower tree transpiration (Bréda, 1999). This condition can improve soil water content, but the effect is offset by the water consumption of the understorey vegetation, which can increase with greater light availability. Light also drives the energy balance of the stand. More light means a significant increase in air and soil temperatures during the day and a small decrease in night temperatures by radiation loss. The net increase in day temperatures and a higher soil water content improve the biological activity of the soil; the humus is therefore of better quality and nutrients are recycled more efficiently. Hence light can be considered as a synthetic indicator of resource availability and microclimate in forests (Barbier et al., 2008).

Light quantity and quality are among the processes that control the success of seed germination and the establishment and growth of tree seedlings in the understorey. The shade-tolerance of young tree species varies according to their successional status, the more shade-tolerant species being potentially better able to regenerate in the dark understorey than the more intolerant ones. Light is consequently a fundamental key to forest regeneration. Light also promotes the development of the ground vegetation, composed of graminoids, forbs, shrubs, and young trees, the composition of which varies with site conditions and overstorey tree species, in addition to light. The understorey vegetation can compete with tree seedlings for resources to varying degrees depending on the species present, and may seriously impede tree regeneration in some cases (Balandier et al., 2006). These understorey plants can intercept a significant fraction of the light in the understorey and so the remaining light available for tree seedlings can vary greatly depending on species and composition of floor vegetation.

The light path into the forest is as follows: the incident light above the canopy is first intercepted by the overstorey trees, and then by the midstorey trees when these are present. The light that reaches the understorey controls the development and composition of the floor vegetation, which in turn intercepts some light. Finally, the tree seedlings use what light remains. The forester has to control this chain of light sharing to direct forest stands towards different objectives. We present here some results on this light sharing chain and their implications for management.

Materials and Methods

Light transmitted by the overstorey and understorey vegetation was measured using different methods. Hemispherical photographs were used to indirectly estimate light transmission through the overstorey of adult trees. The equipment used was a camera fitted with a 180° aperture lens with which it was possible to take a photograph of the whole sky hemisphere, with the zenith at the centre of the photograph and the horizon at the edge. The photograph was taken without direct radiation from the sun, i.e. under full cloud cover, or at sunrise or sunset, which considerably restricted the time periods when photographs could be taken. The camera was set perpendicular to the sky zenith about 1.5 m above the ground, if possible above the understorey vegetation. The principle for computation of transmitted light from the photograph was as follows; the colour photograph was converted into a black (vegetation) and white (sky) picture using a local thresholding procedure (Adam et al., 2007). The ratio of white to black pixels (sky to vegetation) gave the gap fraction from which the transmitted light could then be computed (Adam et al., 2008). The transmitted light could be divided into diffuse light from the whole sky vault using the whole photograph, and direct light from the sun using the fraction of the photograph corresponding to the path of the sun, which could be calculated for any day of the year. The method thus enabled us to compute the transmission of light for the whole year, certain months or a particular day. The drawback of the method is the difficulty obtaining a quality photograph with no over-exposure in which all parts of trees are clearly represented. This is possible only if no direct sun is present on the photograph and the sky is perfectly homogeneous, and the colour pixels are correctly classified into sky and vegetation. This last is the most severely limiting part of the method.

Transmitted light can also be measured directly using light sensors. In many experiments we used either linear (length 1 m) or point light sensors in the total solar radiation spectrum (300-3000 nm) or the PAR spectrum (400-700 nm). Sensors were set 1.5 m above the ground and if possible above the understorey vegetation for at least 24 h, to account for the complete sun path over the entire day. In the same 24 h period a sensor of the same type was set nearby in an open place to measure incident radiation. The transmittance of the forest stand was then calculated as the ratio of light in the understorey to incident light during the 24 h period. This process enabled us to compare, at least to some extent, measurements made on different days of the year (i.e., with different sun flux) and with different weather conditions (i.e., cloudy or sunny). The drawback of the method is that a single day of measurement cannot account for light interception by the overstorey during several months or the whole year, particularly if the canopy is very heterogeneous, i.e., with large gaps where direct sun radiation can reach the ground on some days or in some months in the year.

Light transmitted by the understorey vegetation was measured using a linear PAR sensor of length 80 cm and width 1 cm (Accupar, Decagon). Its long-stemmed shape was easy to slide into the vegetation, generally a few cm above the ground, without disturbing the structure of the plant cover. It was composed of 80 photocells to measure local variations in light interception. In the same way as overstorey transmittance, light recorded under the understorey vegetation is related to a measure of incident radiation during the same period. The drawback of the method is the same as for the overstorey, and a hemispherical photograph is not easy to take from within the vegetation.

Light measured either under the overstorey or under the understorey vegetation was related to vegetation characteristics such as tree height, diameter, basal area, crown characteristics, or herbaceous height or cover.

Results

Light interception by the overstorey

In regular, even-aged stands, composed of a single species, light interception by the overstorey is relatively easy to predict. Light measurements and stand characteristics showed that transmittance (*T*) of the overstorey was related exponentially to stand basal area (*G*), by a Beer-Lambert law (Balandier et al., 2006; Sonohat et al., 2004), $T = \exp(-kG)$, where k is the extinction coefficient: this is a function of species, stand age, and time lag and intensity of the last thinning (Sonohat et al., 2004). Figure 1 illustrates the effect of species identity; for the same stand basal area and age, light intercepted by different species during the leafy period can vary by a factor of 1 to 4.

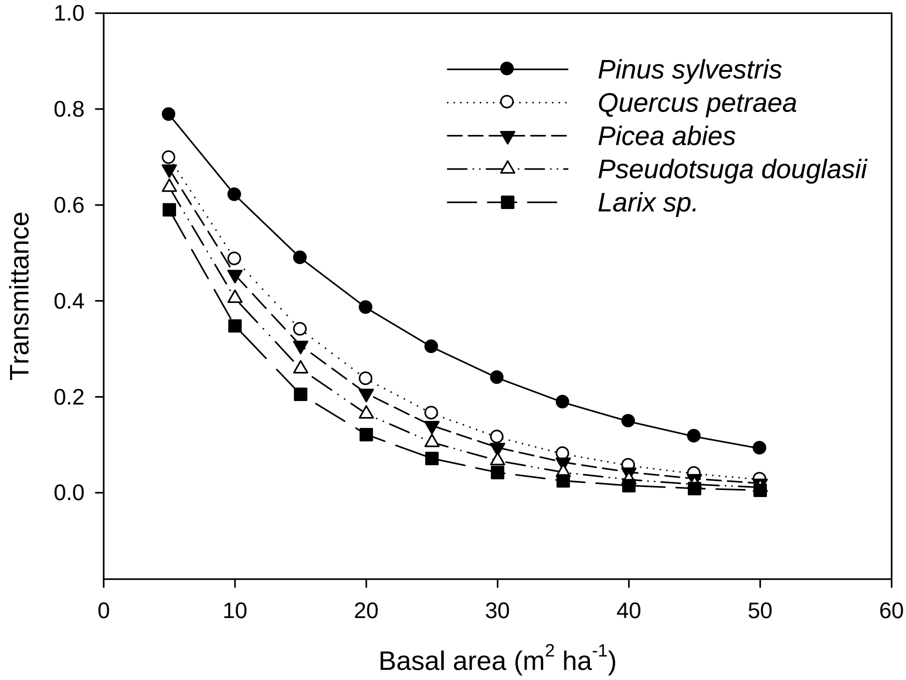

Fig. 1. Simulations of light transmitted during the leafy period by different species according to their stand basal area for stands in France and Belgium. Transmittance is expressed as the quantity of light measured in the stand understorey relative to the incident light above the canopy.

In these regular, even-aged stands, the quality of light, i.e. its spectral composition, can be deduced from measurements of a considered wavelength band as there are relationships between total solar radiation (300-3000 nm), photosynthetically active radiation (PAR, 400-700 nm) and red (R, 660 nm) or far-red (FR, 730 nm) radiation (Balandier et al., 2006). Of particular interest is the R / FR ratio, which drives many plant morphological processes.

In uneven, irregular stands, composed of one or more species, light measurement, prediction and simulation is not easy because of the large gaps in the overstorey canopy, which leads to a very wide variability of transmitted light, in both quantity and quality. In that case, a single variable at the stand scale, such as basal area, is no longer sufficient, and more local variables must be considered such as individual tree size and position, or at least information on tree spatial distribution (Goreaud et al., 2007). The difficulty of the approach is staying at a level of description that allows forest managers to actually use the model, i.e. it must not be too complex, at least for the information required as input. With this in mind, we built a model with a multiscale representation of the forest (Da Silva et al., 2008), i.e. from the tree branch scale, crown scale, tree scale to stand scale, that can be used to study the worsening of light prediction with the scale of representation (Da Silva et al., 2007). This model is being evaluated.

Development and composition of the understorey vegetation

Light availability in the understorey promotes the development of the floor vegetation. Globally, at the community level, there is a logarithmic increase in the vegetation cover with light availability, from no vegetation for very low levels of transmittance (≅ 0.02) to a maximum for an asymptote of 0.4 of transmittance, which means that increasing light above this value does not correspondingly augment vegetation cover or biomass (Balandier & Pauwels, 2002). At the species level, patterns of plant cover or biomass with light availability are not simple and depend on the light requirements of species. For example, a recent study showed a near-linear increase in *Cytisus scoparius*, a light-requiring species, with light availability, whereas *Rubus idaeus*, a more shade-tolerant species, showed a bell-shaped curve in response to light, with a maximum cover for a transmittance of 0.45 (Gaudio et al., 2008). We are studying the response patterns of other common species that colonise gaps in temperate forests, such as *Rubus fruticosus*, *Molinia caerulea*, *Calluna vulgaris* and *Pteridium aquilinum*.

Light availability modifies not only the cover of the floor vegetation but also its species composition. However, the response pattern of species composition with respect to light is not simple. Some studies have reported a bell-shaped curve with a maximum number of species for intermediate light levels (e.g., Balandier & Pauwels, 2002), others a continuous increase in species richness with light. The first response is observed more frequently at a local scale, whereas the second is often recorded for larger geographical scales (Rajaniemi, 2003). The bell-shaped curve from shade to full light is explained by the progressive enrichment of a flora made up of shade-tolerant species by more and more light-requiring species as light increases up to a maximum species richness; thereafter one or more monopolistic, strongly light-requiring species colonise the whole space at the expense of all the other species. In terms of tree regeneration management, those monopolistic species (e.g. *Rubus fruticosus*, *Molinia caerulea* and *Pteridium aquilinum*) are highly competitive for resources and can jeopardise tree seedling establishment and growth.

Light interception by the understorey vegetation

Depending on their development, the understorey plants can intercept a non-negligible amount of light (fig. 2). For example, the transmitted light recorded under *Cytisus scoparius*, *Rubus fruticosus*, and *Epilobium angustifolium* can be as low as 0.01, 0.03 and 0.05, respectively (Sivade, 2005). These are very low values, which can seriously compromise tree regeneration when tree seedlings are small and surrounded by such species. Another study on *Rubus fruticosus* for different stands in France and England suggested that transmittance could range from 0.5 to less than 0.02 for plant LAI values ranging from 0.5 to 4, respectively (unpublished data).

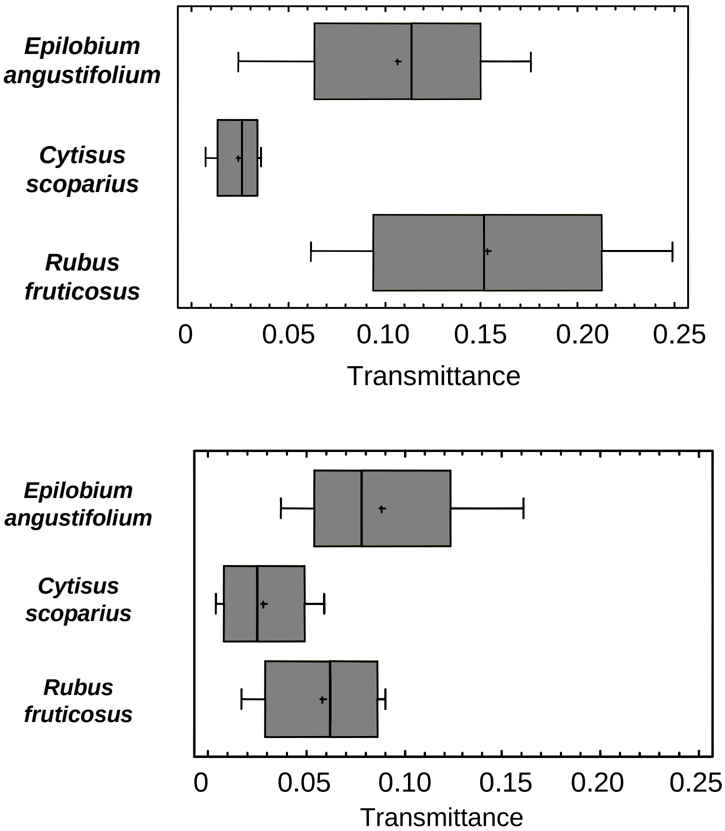

Fig. 2. Light (PAR) transmitted to soil level by three common plants colonising gaps in temperate forests in May (top) and July (bottom) 2005 at different sites in uplands of central France (for each species the centre box covers 50% of the data, the vertical line in the box being the median).

Discussion: implications for tree regeneration

Tree seedling establishment and growth are affected to varying degrees by light availability according to species shade-tolerance; for example *Fagus sylvatica*, a late successional shade-tolerant species, is able to survive and grow under very limited amounts of transmitted light, as low as 0.03. It grows more vigorously with increasing light up to a value of about 0.4, beyond which no further improvement in growth is usually seen (e.g. Balandier et al., 2007). By contrast, an early successional species that is not very shade-tolerant, such as *Pinus sylvestris*, needs more light to establish and grows more vigorously with more light linearly up to a transmittance of 1. Hence forest managers have to run the stand differently, especially as regards thinning operations, to regenerate and promote particular species. However, as shown above, depending on the light availability in the understorey, vegetation of varying density can develop and intercept a large amount of the available light (in addition to water and nutrients, Balandier et al., 2006). This understorey vegetation, depending on its density and species composition, can strongly compete with tree seedlings, severely impeding their growth, or even causing their death (Balandier et al., 2008; Coll et al., 2003; Provendier & Balandier, 2008). Therefore the forest manager has to find a compromise between a light level that promotes optimal tree seedling growth, but also generates a dense competing layer of understorey vegetation that can jeopardise tree regeneration, and a very low light level that prevents all understorey plant growth, including tree seedlings. The point of equilibrium that allows significant tree seedling growth while preventing too-dense understorey vegetation is often also the point where species richness is at its maximum; for a natural sustainable management, this point should be sought by forest managers adjusting light sharing among the different strata of the forest.

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